TEMPERATURE AS A FACTOR IN THE DEVELOPMENT OF ANTS.

With Further Observations on Ants Deprived of Food.

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Some recent experiments made by me lead to the conclusion that temperature is a dominant factor in the development of ants; that, other things being equal, it determines the time of the deposit of the eggs, the length of the larval period, and the hour of exit from the cocoon; and that the developing young of unlike species of ants are differently affected by the same degree of heat. It also appears probable that unlike species of ants develop and deposit their eggs at different temperatures, fixed for each species.

The greater activity of the adult ants in higher temperatures, with the increased movement of the anterior end of the larva which may be observed when the temperature rises, and the quickening of the pupæ which occurs in the hottest days, are doubtless an effect of the stimulation of metabolism by heat.

Experiment A.

My N. queen *Camponotus pennsylvanicus* laid eggs in the first week in August, 1903, which were kept in my living room where the temperature seldom rose above 70° F. or 21° C., and the earliest ant to issue from these eggs hatched on April 25, 1904, when the temperature had risen to 78° F. or 26° C. On July 14, 1904, I removed this queen to a new nest, where she was kept at a temperature that seldom rose above 70° F., and she laid no eggs until after I had, on November 20, 1904, removed her to a room where the usual temperature was from 82° to 85° F., rarely falling to 70° F. and occasionally rising to 90° F. On December 2 I observed twenty eggs, which had increased to sixty on December 11. The first larva appeared on December 18. On December 30 all the eggs had hatched and there were several tens of larvæ. The first cocoon was spun on January 8, and the

first callow appeared on January 29, 1905. This indicates about twenty days for incubation, a month for the larval and twenty days for the pupal period, all at a time when the congeners of this queen were merged in winter repose.

This N. queen shared the labors of the workers in the care of the young, which continued to develop until the 26th of March, when I removed the nest to a room having a fairly steady temperature of 70° F. At this temperature the remaining cocoons failed to hatch, and the fifty larvæ ceased to grow. The larvæ did not increase in size till the last days of the following June, after the temperature had risen to 76° F. The first cocoon of this newer brood was spun August 6, 1905.

Although this queen had deposited eggs in March, 1904, she deposited none in March, 1905, nor did she lay any thereafter until July 26, 1905, when she again deposited a few eggs. During the first week in August, 1905, the eggs were increased to about the same number that she had laid at the same season two years previously. Her failure to lay eggs in August, 1904, was doubtless due to the agitation consequent upon her service in several of my experiments at about that time. I have often observed that psychic influences affect the deposit of eggs by ant queens. Her failure to lay eggs in March, 1905, was probably due to exhaustion consequent upon the work to which she had been stimulated by high temperature in the previous December.

Since the food supply, the humidity, and the number of workers were factors whose variation was but slight in the nest of this queen, it appears probable that the time of the development of eggs and the growth of the young was determined mainly by the temperature.

Experiment B.

My *Cremastogaster lineolata* queen laid hundreds of eggs in August, 1904, and the larvæ therefrom grew scarcely at all until, on November 20, 1904, I removed her nest from a room where the usual temperature had been 70° F. to a chamber where the temperature was usually from 82° to 85° F. Early in December the larvæ began to increase in size and on December 22 the first pupa appeared among them. The young continued to thrive and fifty-three pupæ had been developed in the nest before March

26, 1905, when I removed the nest to a room having a usual temperature of 70° F. No more pupæ developed thereafter until late in the succeeding summer. The larvæ remained in a state of arrested development from the end of January until the end of the following June, when, under the influence of the natural rise in summer heat, they entered upon a period of renewed growth and in August presented me with ten more pupæ.

This queen laid eggs in June, when the temperature rose to 75° F., and continued to deposit them at various times throughout the summer.

EXPERIMENT C.

A group of thirty workers, majors and minors, of *Camponotus herculeanus pictus* hatched between July 11 and 31, 1904, were kept at the temperature of 70° F. or 22° C. until November 20, when they were removed to a chamber whose usual temperature was from 82° to 85° F. or 28° to 30° C. On March 26, 1905, they were returned to their place in my living-room, where the temperature was usually at 70° F. They laid no eggs until May 14, and then deposited about fifty before June 4, 1905, apparently under the influence of a rise in the temperature to 78° F. or 25° C.

The age of these ants may, however, have had influence on the time of egg-laying. It would be interesting to ascertain, by dissections of worker-ants, whether differences in the degree of development of the ovaries in workers of the same species is correlated with difference of age in the respective workers. It may be that the ovaries of many worker-ants do not develop until some months, or until the second season, after hatching.

EXPERIMENT D.

A group of fifty workers, *Formica argentata* hatched during September, 1904, were kept by me at a fairly steady temperature of 70° F., and laid no eggs until after they were removed to a chamber having a usual temperature of from 82° to 85° F. Their first egg was deposited on January 1, 1905, and during the ensuing week the eggs increased rapidly in number, so that on January 8 there were more than one hundred. The first larva was observed on January 15. None of the larvæ reached the

pupa-stage, and all these eggs and their issue had disappeared before March 19. On March 26 this nest was removed to a room having a temperature of 70° F., and these ants ceased from egg-laying until the temperature again rose to more than 80° F. in the following July. The young larvæ from the July eggs rapidly disappeared in the intense heat of July, 1905, and only five of them spun cocoons. It seems that the development of the eggs of this species demands a high temperature, while the development of the larvæ requires a lower degree of heat.

Dr. Irving A. Field, keeping a nest of one hundred and fifty worker-ants of this species, at Harvard University, gives me the following account of said nest: "The ants all hatched between August 20 and September 23, 1904. They laid no eggs until after November 30, when the nest was placed in a chamber having a temperature of from 75° to 85° F. Between December 30, 1904, and January 9, 1905, about a hundred and fifty eggs were laid, all of which were subsequently addled or else were eaten by the ants. But between June 6 and 13, 1905, about sixty eggs were laid, and from these, in natural summer temperature, many larvæ safely passed to the pupa-stage."

Experiment E.

I had one group of virgin workers of *Stenamma fulvum* two years old; one group of virgin workers of *Stenamma fulvum* one year old; and one group of virgin workers of *Camponotus americanus* newly hatched, that deposited no eggs during September, October and November, 1904, when they were kept at a temperature of about 70° F. But in all three of these groups, eggs that produced larvæ were deposited between November 20, 1904, and March 26, 1905, when they were kept at a temperature of from 82° to 85° F.; and all were again subjected to a completely arrested development of the young when the temperature fell to 70° F. between the end of March and the middle of June, 1905.

Groups of virgin workers of *Formica Schaufussi* and of *Formica neogagates*, housed, fed, and kept at the same daily temperature as were the above named ants, laid no eggs during either the

periods of low or of high temperature, but deposited eggs after the middle of June, 1905, when the summer heat rose to 78° F.

Other Experiments.

Dr. Field had a nest of workers of *Formica pallide-fulva fuscata* in which many eggs were deposited in March, 1905, when kept at a temperature of from 75° to 85° F. and the issue of these eggs passed safely through the larval and pupal stages at the same temperature. Dr. Field had also a nest of *Camponotus pennsylvanicus* workers who failed to rear their larvæ to pupation in the summer of 1904, but who, under the influence of the above named high temperature brought three to pupation in January, 1905.

Dr. W. M. Wheeler writes to me that *Formica consocians* workers in his artifical nests deposited many hundreds of eggs, in March, 1905, in a room whose temperature never rose above 60° F. or 15° C.

It appears that the time of development may be altered by change of the prevailing temperature and that an intervening period of recuperation will be maintained in spite of a continued temperature-stimulus. Other factors being equal, the development of the eggs within the ovaries, the deposit of the eggs, the feeding and growth of the larvæ, the pupation and the hatching, all appear to be determined by temperature. The degree of heat suiting the species probably varies for the different stages of development.

All the ants involved in my experiments had the same food-supply, the same daily temperature, and similar housing. They were abundantly provided with insect-food and with a variety of sweets. They always appeared to be in excellent health, and hardly any deaths occurred in any of the nests mentioned. It is therefore difficult to refer behavior so varied to other cause than the varying effects of the same temperature on unlike species of ants, or to avoid the inference that in different species the young develop best at different degrees of heat.

Among the ant-young observed by me, none has developed at a temperature below 70° F.; while long exposure to a degree of heat above 90° F. manifestly causes injury. Two minutes ex-

posure to a temperature of 122° F. or 50° C. will kill the most vigorous adult.

Further Observations on Ants Deprived of Food.

Among the groups mentioned in my paper on "Tenacity of Life in Ants" (in the Biological Bulletin, Vol. VII., No. 6, Nov., 1904, p. 300) were seven *Formica subsericea* workers that had been deprived of food three months and remained alive at the time of writing. These seven ants had been picked up from a roadside where they were foraging under a linden tree, on July 3, 1904. They were kept in a Petri cell containing only themselves and a bit of sponge saturated with water. Cell and sponge were cleansed with alcohol at intervals never exceeding four days, until the end of September, after which time the cell and sponge were cleansed only once a week. No growths were at any time visible under a lens magnifying ten diameters.

On February 3, 1905, one of these ants was removed for dissection, after an enforced fast of just seven months. One died on November 27, one on November 29, 1904; one on February 17, one on February 19, one on March 14, and one on March 28, 1905, the latest survivor having lived nearly nine months without food.

A *Camponotus Americanus* worker, under like conditions, lived without food from July 13, 1904, to February 12, 1905, just seven months.

Two sister queens, *Camponotus Americanus*, one deälated, one winged, under the same conditions, lived without food from July 13 to December 6, 1904, both dying on the same day. These queens had been bred in an artificial nest, and may have lacked the stamina of untamed ants.

After the first of October, all these fasting ants were kept at a fairly steady temperature of 70° F. or 21° C.

Until the day of death the ants walked about, reacted normally to light and heat, and gave no evidence of failure in any of the senses.

In spite of the prolonged fast, there was no fighting nor cannibalism in any group of these ants, and the bodies of those that had died were always found to be intact.

The ability of ants to survive a submergence of several days in water explains their persistence in areas where freshets periodically exterminate all other land insects, and their power to live for many months without food explains their occupancy of places subject to long droughts that destroy their whole food-supply.

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